

NEW INFORMATION ON THE FORAMINIFERAL GENUS *PFENDERINA*

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ABSTRACT. *Pfenderina neocomiensis* (Pfender 1938) is redescribed from loose specimens for the first time and a new species, *P. trochoidea*, is described. *Kurnubia palastiniensis* Henson 1948, *Valvulinella wellingsi* Henson 1948, and *Valvulinella jurassica* Henson 1948, are united in the genus *Kurnubia* Henson 1948. *Kurnubia*, *Pfenderina* Henson, and *Meyendorffina* Arouze and Bizon 1958, are placed in the new family Pfenderinidae of the superfamily Lituolidea. This family is distinguished from the family Verneuilinidae, subfamily Ataxophagmiinae, by the numerous chambers per whorl, finely cribrate aperture and details of internal structure and from the family Orbitolinidae by the finer texture of the endoskeleton, the lesser development of the uniserial stage as compared to the spiral stage and details of the internal structure.

P. neocomiensis occurs in Europe only in the Valanginian and Berriasian, but in the Middle East it is typically found only from the Bathonian to the Argovian. The differing distribution in the two areas is so far without satisfactory explanation.

DUE to the discovery in beds of soft limestone of numerous well-preserved and separable specimens of *Pfenderina neocomiensis* (Pfender 1938) and a new species, *P. trochoidea*, we are able to describe *Pfenderina* fully for the first time. This form has previously been found only in hard limestones.

Comparing these two species with other Foraminifera, four other species show close similarities. These are *Kurnubia palastiniensis* Henson 1948, *Valvulinella wellingsi* Henson 1948, *V. jurassica* Henson 1948, and *Meyendorffina bathonica* Arouze and Bizon 1958.

While placing two of the above Jurassic species in the Carboniferous genus *Valvulinella* Schubert 1907, Henson remarked that '. . . certain details may require classification (of *V. wellingsi*) as a new genus when more is known of its ancestry'. Now that the structure of *Pfenderina* is much more fully known, the taxonomic position of the Jurassic species previously assigned to *Valvulinella* becomes apparent. As will be seen, these species do not belong to that genus, but may be assigned to the genus *Kurnubia* Henson 1948. Further, it arises that the genus *Kurnubia* is no longer to be assigned to the family Trochamminidae. *Pfenderina* has elsewhere rightly been linked with *Kurnubia* and the Jurassic '*Valvulinella*' spp. Sigal (1952), although retaining Henson's classification, drew parallels between these genera and both the family Orbitolinidae and the family Verneuilinidae, subfamily Ataxophagmiinae. Arouze and Bizon (1958) placed *Meyendorffina* in the Orbitolinidae. We consider that *Pfenderina*, *Kurnubia*, and *Meyendorffina* form a very close group, both morphologically and stratigraphically, that is sufficiently distinct from the families Verneuilinidae and Orbitolinidae to be recognized as yet another family, although it is related to both.

The Pfenderinidae are confined to one sedimentary facies group of clean, shallow-water limestones, but seldom occur in the shallowest sediments such as contain abundant oolites. In Europe derived limestone fragments have been described in association with occurrences of *Pfenderina*. Murat and Scolari (1956) described the facies in which *Pfenderina* occurs as 'recifal'. However, there is no indication of biohermal or biostromal

origin of the beds in which Pfenderinidae occur, either in Europe or the Middle East. The Pfenderinidae are usually most abundant in limestones originally of fine grain. In such of these limestones as are little altered, few individual crystals can be clearly resolved at a magnification of $\times 40$ linear. The shell material in such cases, although mostly darker than the rock matrix, is of similar grain, but a more transparent epidermal 'vitreous' layer has been observed in some species. In our specimens there has often been growth of small rhombic crystals, probably of dolomite, indifferently in the matrix and in the shell material. These crystals are most conspicuous when formed in the darker shell material of a test. In all recorded occurrences, whether in a hard or soft limestone, the Pfenderinidae have been diagenetically affected to some extent and all published figures are to some extent obscure because of it. Ours are not free from this defect, but it is marked in Pfender's original figures of *P. neocomiensis*; Pfender (1938) referred to the 'aspect guilloché' of the chamber walls. In some parts of the chamber wall this appearance is entirely due to the secondary growth of crystals, but a similar appearance is also caused by the perforations of the apertural part of the septa and by the labyrinthic passages in the endoskeleton of the central part of the chamber (see below). The original nature of the shell material is therefore often difficult to determine, but we believe that in the best of our own specimens the original microgranular texture has been comparatively little altered, and the fine texture in these cases is similar to that of many other Lituolidea. It is difficult to be sure that there were never any agglutinated grains in the test, but it is most likely that all seeming inclusions are the result of secondary recrystallization.

In Europe *Pfenderina* has been recorded from France and Switzerland in beds of Berriasian and Valanginian age but never from the Jurassic. In the Middle East *Pfenderina* is recorded from the Bathonian to the Argovian (Oxfordian) with its greatest abundance in the Bathonian and Callovian. Records of younger age are suspect and even if any are eventually substantiated, they relate to rare occurrences. In both southern Europe and the Middle East there are both Upper Jurassic and Neocomian limestones indicative of an environment suitable for *Pfenderina*. It has been thought that both areas, lay in the same faunal province and in the same major depositional basin. We can detect no significant difference between the specimens of *P. neocomiensis* from the two areas, and from published information it seems most unlikely that any substantial error has been made in dating any of the relevant beds in either region. The peculiarly varying distribution of *P. neocomiensis* therefore presents a problem.

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The figured specimens have been deposited in the British Museum (Natural History). The relevant registration numbers are given in the plate explanations.

Family PFENDERINIDAE NOV.

Diagnosis. The shell material is microgranular, without detectable agglutinated material. The early chambers are always spirally arranged and many per whorl. The chamber arrangement sometimes produces a low trochospire throughout. Occasionally the test is almost or quite planispiral, but more often the arrangement tends to become helico-

spiral. The later chambers may be uniserially arranged. The chambers are low; in low trochospiral tests they are unequally equitant; in helicospiral tests they are nearly oval and each occupies most of the area of the base; when uniserially arranged they are circular and slightly dished. The apertural face has a large, finely perforate, central area which constitutes a cribrate aperture. The peripheral part of the apertural face is imperforate and corresponds to an outer zone of the chamber which may be empty or have a partial subdivision into subepidermal cells. The part of the chamber behind the apertural area is filled with endoskeleton, originally labyrinthine but sometimes remaining so in the later chambers only. A secondary intercameral foramen is present in the form of a slit or circular aperture near the margin of the infilled part of the chamber. No corresponding external aperture has been observed. In helicospiral and uniserial developments the infilled parts of the chambers aggregate to form a columella. In low trochoid tests the columella cannot form but there is a homologous spiral structure.

Affinities with other families. Henson (1948) classified these foraminifera in the Family Trochamminidae, but this was a formal decision taken to avoid disturbance of the existing classification of *Valvulinella* Schubert 1907 and he recognized that this was possibly a temporary expedient. In this paper we take the general outline of the family classification from Sigal (1952) who, although he retained Henson's classification formally, indicated parallels between the genera now ascribed to the Pfenderinidae and those of both the Orbitolinidae and the Verneuilinidae, especially of the subfamily Ataxophragmiinae. The members of both these families typically have agglutinated shell material and therefore appear very different from the Pfenderinidae. However, in both families there are species of the type genus which lack agglutinated grains. The Verneuilinidae are typically strongly trochospiral, tend to reduce the number of chambers per whorl and usually have a single aperture. In species with a cribrate aperture, it is usually possible to trace its derivation from a single one. The Pfenderinidae have many chambers per whorl, never two or three, although they may have a uniserial terminal stage. The apertural pores are fine and numerous. The chambers are low, while those of the Verneuilinidae tend to be high and globose. The two families contain certain morphologically similar genera, but the various differences of internal and external organization indicate that the resemblances are due to homoeomorphic developments arising in distinct stocks. The fine texture of the central zone of the chamber is distinctive of the Pfenderinidae. The genera of the Orbitolinidae also have resemblances to the Pfenderinidae which cannot be lightly dismissed. If it were considered that the separation of the family Pfenderinidae was not justifiable, we should place these foraminifera in the Orbitolinidae. These two groups have certain features in common. Where subepidermal partitions are present, the nature of these is very similar. In both families the typical aperture is cribrate with numerous fine pores. The part of the chamber behind this porous area is occupied by endoskeleton that is penetrated by labyrinthine passages in *Orbitolina* and in the Pfenderinidae. But those of the Pfenderinidae are finer and may become secondarily infilled. The more typical Pfenderinidae have the trochoid development of the spire to distinguish them from the Orbitolinidae; *Orbitolina* itself has a plane initial spire in the microspheric form (although some textbooks state otherwise; Douglas 1960) and a helicoid spire is not usual until Tertiary species such as *Dictyoconus indicus* appear. But the variation from trochospiral towards

planispiral seen in *Pfenderina trochoidea* and the near planispiral arrangement in *Meyendorffina* prevent us from using the manner of coiling of the spire as a diagnostic character. The dominance of the uniserial stage over the spiral stage and the habit of rapid increase of chamber diameter in the Orbitolinidae also distinguish them from the Pfenderinidae, but this, too, cannot be taken to be a truly diagnostic character, for some species of the Pfenderinidae do show a well-developed uniserial termination. The Pfenderinidae have intercameral foramina which, together with spiral grooves or open spaces connecting them, form very characteristic structures not observed in the Orbitolinidae. This is certainly one of the more striking differences between the members of the two families, but it cannot be concluded from this feature alone that they are far apart genetically.

In brief, the creation of the new family Pfenderinidae is suggested because the species concerned have so many features in common as to indicate that they belong to one restricted branch of descent. At the same time it is suspected that this branch is not far removed from others, especially that of the Orbitolinidae. It so happens that known Pfenderinidae have such stratigraphic distribution as to support the idea that they are a natural group. One anticipates difficulty in determining lines of descent from ancestral species in which differentiation between the Pfenderinidae, Orbitolinidae, and Verneuiliidae was incomplete.

Distribution. The Pfenderinidae are known from the Bathonian to the Valanginian. They have been reported from Europe, North Africa, and the Middle East. They occur only in shallow-water limestones.

Genus PFENDERINA Henson 1948 (1947)

Type species. *Eorupertia neocomiensis* Pfender 1938.

Description. The shell material, as seen in fossil specimens, appears microgranular and dark in thin section, excepting sometimes for a thin epidermal layer of 'vitreous' appearance. It is believed that these appearances reflect very nearly the true nature of the original shell substance and that there was never any agglutinated material. Small calcite and dolomite rhombs commonly observed within specimens are believed to be of diagenetic origin. Except for apertural pores the chamber wall is imperforate.

The test is spiral, varying from strongly helicoid to almost planispiral. In the known species almost equal numbers of individuals are dextral and sinistral. There are numerous chambers per whorl. Typically the chambers are low and rather oval, each occupying a considerable part of the base and overlapping the axis of coiling. An outer, crescentic part of the chamber is empty and the part of the septum covering this is imperforate. The large remaining inner part of the chamber is occupied by endoskeleton in which there are labyrinthine passages and the corresponding part of the septum is perforated by the pores of the cribrate apertures. Where the chambers are appropriately arranged, in a high trochoid or helicoid spire, the aggregation of the infilled parts of the chambers forms an axial columella. In the variants tending most towards being planispiral the chambers are unequally equitant and cannot form a straight columella. A homologous spiral structure is then formed. In the earlier chambers of the test the labyrinthine passages were infilled during the life of the organism and the columella or

homologous spiral structure is solid in this part. A secondary intercameral foramen is present in each septum in the form of a circular aperture. These foramina lie in what amounts to a spiral groove in the margin of the columella. No corresponding external aperture has been seen.

Affinities with other genera. Arising from our studies of *Pfenderina* and many specimens from various localities of the Jurassic species of *Valvulinella*, we see no real objection to placing the Jurassic species which were tentatively assigned to *Valvulinella* by Henson (1948) in the genus *Kurnubia* Henson 1948. As was recognized by Henson, the link is very weak between the Jurassic species, *Valvulinella jurassica* and *V. wellingsi*, and *Valvulina youngi* Brady 1876, the Carboniferous type species of *Valvulinella* Schubert 1907, for the latter lacks a columella. *V. jurassica* and *V. wellingsi* could, in our opinion, very well be transferred to *Kurnubia*. It might be objected that this involved including in one genus species with and without a terminal uniserial stage. However, the three species, so highly specialized in some respects, are at present shown to differ only in minor details of chamber shape and arrangement, according to which there may or may not result the development of a uniserial termination. For this reason we would include the three species in the same genus at this time, though we would note that further studies of really good specimens of the type species, *K. palastiniensis*, might eventually reveal features which would justify the distinction of two genera.

Accepting the above, the diagnostic distinction between *Kurnubia* and *Pfenderina* is the lack of subepidermal partitions in the latter. There are other distinctive features. In all known species the columella is proportionally smaller in *Kurnubia* than in *Pfenderina*. It seems that *Pfenderina* was the ancestor of *Kurnubia* and that decrease in the size of the columella was an evolutionary trend which accompanied the development of subepidermal partitions. In *Kurnubia* there appears to have been little or no secondary infilling of the labyrinthine passages of the columella. In *Kurnubia* the secondary foramina lie just outside the columella whereas in *Pfenderina* they are aligned with spirally arranged depressions in the margin of the columella. There can be no doubt, however, that the genera are closely related.

Meyendorffina has all the characteristics of the Pfenderinidae in chamber structure and general appearance, but is planispiral, or nearly so. In this it contrasts with the more typical, elongate-trochospiral Pfenderinidae, but does not differ markedly from the more planispiral variants of *Pfenderina*. It is terminally uniserial, as is the case with one species of *Kurnubia*. Arouze and Bizon (1958) placed *Kilianina* in the family Orbitolinidae, in association with *Meyendorffina*. Its structure of chambers about an open umbilical space is not comparable either in the Orbitolinidae or the Pfenderinidae. We would place this genus provisionally in the family Trochamminidae, subfamily Tetra-taxinae.

Distribution. *Pfenderina* has been recorded from the Bathonian to the Valanginian.

Pfenderina neocomiensis (Pfender)

Plate 73, figs. 1-9; Plate 74, figs. 1-3; Plate 75, fig. 1; Text-fig. 1, A-D.

Eorupertia neocomiensis Pfender 1938.

Pfenderina neocomiensis (Pfender); Henson 1948 (1947).

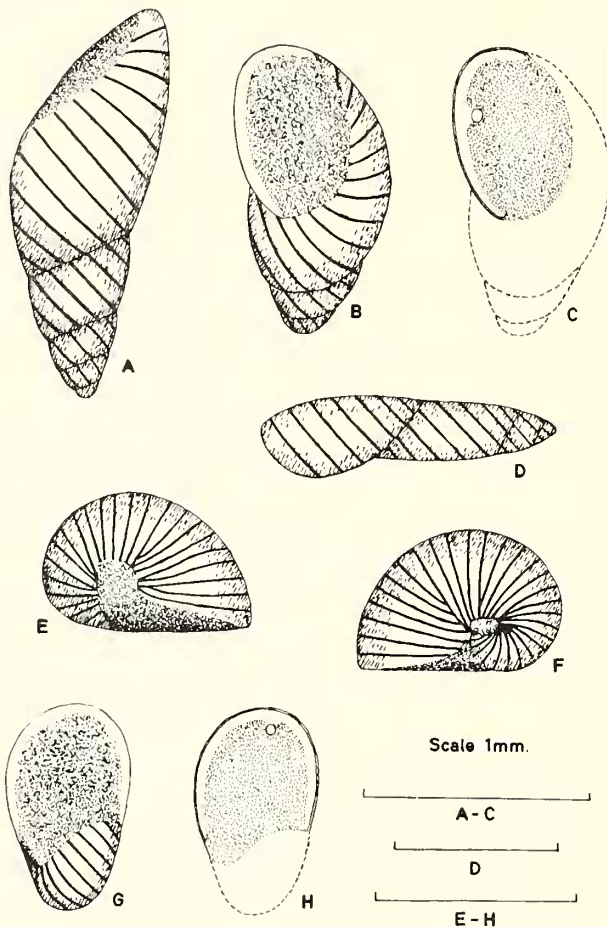
Pfenderina neocomiensis (Pfender); Murat and Scolari 1956.

Pfenderina neocomiensis (Pfender); Marie and Mongin 1957.

Pfenderina neocomiensis (Pfender); Hudson 1958.

Pfenderina neocomiensis (Pfender); Hudson and Chatton 1959.

Material. One hundred and twenty-six separate specimens and twenty thin sections from samples from deep bore-holes on the Qatar Peninsula of Arabia and bore-hole Najmah No. 29, Iraq. Figured specimens: P. 43713, 43719-25, 44639-40.



TEXT-FIG. 1. A-D, *Pfenderina neocomiensis* (Pfender). A-B, Two external views of the same specimen. C, Reconstruction corresponding to B of the relationship of the crescentic chamber space, endoskeleton and foramen in the last chamber. Labyrinthic passages not shown. D, External view of another specimen. E-H, *Pfenderina trochoidea* sp. nov. E-G, Ventral, dorsal, and apertural views of the same specimen. H, Reconstruction corresponding to G of interior of last chamber.

Description. The test rarely exceeds 2 mm. length, usually being about 1.5 mm. The width varies from 0.5 to 1.0 mm. The apex is usually acutely conical but in some specimens is more rounded. In all cases the angle of the spire decreases in later whorls. The last two whorls may show negligible increase in diameter. The adult test usually has 4 to 5 whorls

with 14 or more chambers in the last whorl, the greatest number seen being 20. Features of dimorphism have not yet been detected. The spiral suture lies in a groove and the septal sutures are very weakly indented. The septal sutures are at right angles to the spiral suture and in later whorls both are at about 45° to the axis of coiling. The septal spacing is about 0.1 mm. and the whorl height, measured in the direction of the axis, is about 0.6 to 0.8 mm. in the fourth whorl. The part of the chamber wall exposed between septal sutures is imperforate. The apertural face is roughly oval and slightly convex. There is an outer imperforate rim over the crescentic space within the chamber and the rest of the apertural face is finely perforate. The chambers all overlap the ventral pole of the axis of coiling and each therefore occupies most of the base, which is very obliquely set to the axis. Each chamber has an outer crescentic space without internal structures, but the central zone behind the apertural area is infilled with endoskeleton, the material of which has the same appearance as, and is continuous with, the material of the adjoining chamber wall. In the last two or three chambers, and sometimes in a few earlier chambers, labyrinthine passages can be seen within the endoskeletal material, but in the earliest chambers these passages become secondarily filled with material that has the same optical properties as the remainder of the endoskeleton. The endoskeletal material thus becomes aggregated into a columella that appears quite solid. In each septum there is a round intercameral foramen, placed at a point about equidistant from the ends of the crescentic chamber spaces. The foramina lie in line with notches in the outer margin of the endoskeletal material and these notches together give the appearance of a spiral groove around the outside of the columella. The foramina seem to have been formed secondarily because no trace of a similar aperture has been seen on the apertural face. The appearance of the intercameral foramina in a decorticated specimen recalls that of the tunnel in the Fusulinidae, but the resemblance is, as far as we can tell, fortuitous.

Remarks. Our specimens, on the average, seem to show less inflation of the chamber walls and more infilling of the labyrinthine passages than Pfender's original specimens, but the differences are too slight to be regarded as significant.

Distribution. Europe. Known from the Berriasian-Valanginian 'marbre bâtard' of southern France and western Switzerland. Pfender described *P. neocomiensis* from the Valanginian of Provence. Murat and Scolari (1956) gave a careful summary of occurrences in France and Switzerland known to that date and Dufaure (1958) gave further records from France. All agree in dating the occurrences as Berriasian or Valanginian and investigations on the Upper and Middle Jurassic of that area are adequate to create the strong presumption that the species is absent from pre-Neocomian beds in Europe.

Middle East. Known from the Shuqra formation (Oxfordian) of south-west Arabia; the *Shuqraia* beds (Oxfordian) of Kurnub, Palestine; the upper part (Callovian to Oxfordian) of the Lower Musandam Limestone of Jebel Hagab, Oman; the Uwainat member and lower parts of the Araej formation (Bathonian) of Qatar; the Najmah formation (Callovian-Oxfordian) of Iraq. The ages cited are taken from Hudson (1954), Hudson (1958), Hudson and Chatton (1959), and Dunnington (1960). The evidence for the dating of the Araej formation will appear shortly (Sugden, in press). Hudson and Chatton (1959) recorded Jurassic occurrences as *Pfenderina* sp. because at the time that their publication was prepared *P. neocomiensis* and *P. trochoidea* had not been differentiated. *Pfenderina* is also reported from the Muhawir formation (Bathonian) of

north-west Iraq (Dunnington 1960) where *P. neocomiensis* is probably present, but the specimens are too poor for certain specific identification.

Doubtful records exist of *Pfenderina* in the Riyadh group (Kimeridgian) and Thamama group (Valanginian) of Qatar (Hudson and Chatton 1959) and from the Cenomanian of Jebel Abd el Aziz, Syria (Henson 1948). On these reported occurrences we would comment that the records need verification. If any are indeed true they refer to very rare occurrences and we would note that when dealing with rare and poorly preserved material it is easily possible to confuse *Pfenderina* with various other superficially similar genera.

Pfenderina trochoidea sp. nov.

Plate 73, figs. 1-7; Plate 74, figs. 3-6; Plate 75, figs. 1-3; Text-fig. 1, E-H.

Holotype. P. 43728. Figured specimens: P. 42967, 43710-16, 43726-31, 44641.

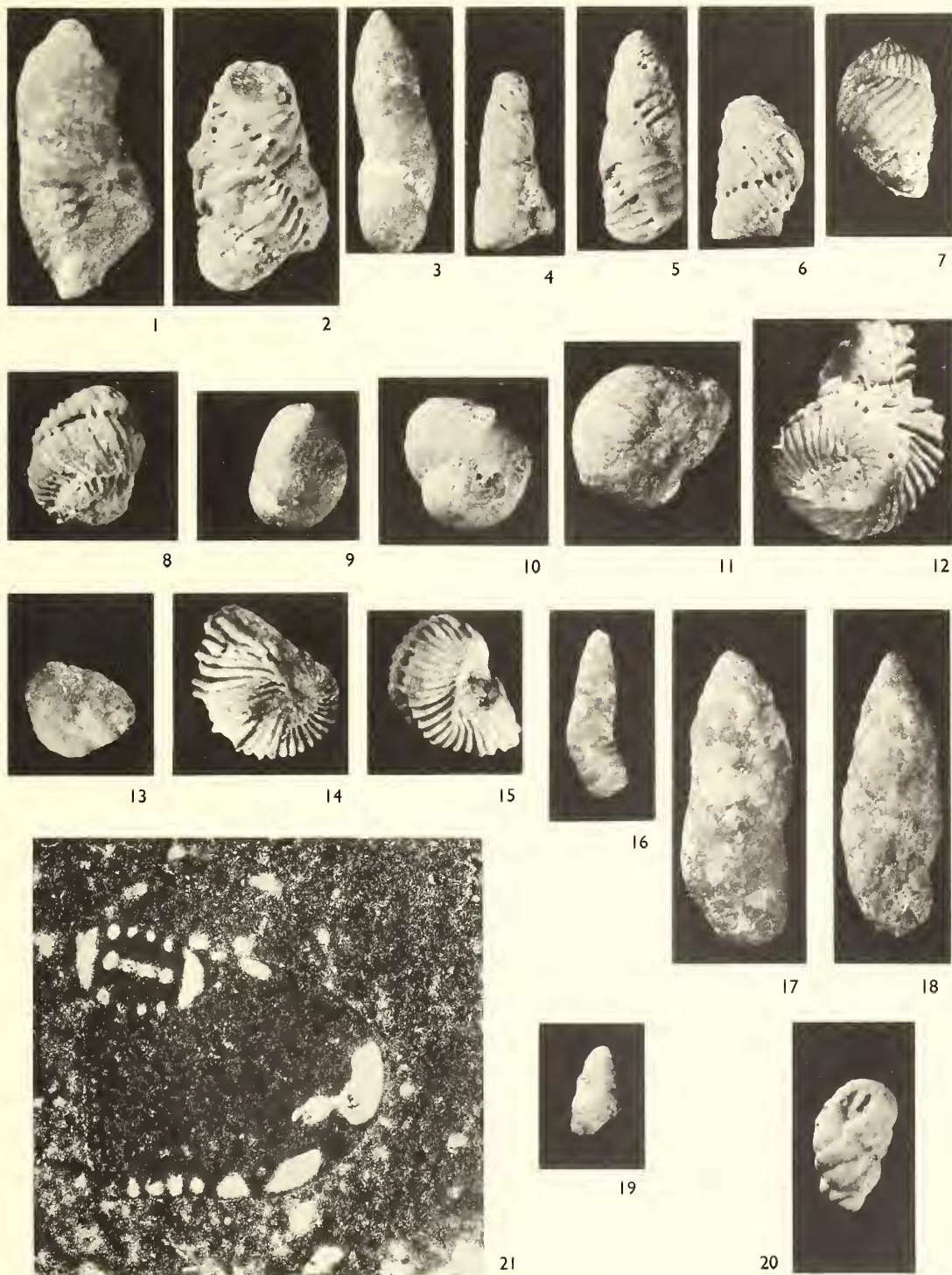
Type locality. The Uwainat member of the Araej formation in deep bore-holes of Jebel Dukhan, Qatar Peninsula of Arabia. Additional locality: lower part of the Najmah formation in deep bore-hole Najmah 29, Iraq.

Material. One hundred and thirty-one separate specimens and eight thin sections.

Description. The test rarely exceeds 1 mm. in axial length; the maximum diameter may attain 1.5 mm. and often exceeds 1 mm. while the smaller diameter, at right angles to this, is usually smaller than 1 mm. The spire is typically low trochoid with slight dorsal overlap but strong ventral involution. However, in some specimens the spire is almost plane and in such cases the chambers are unequally equitant. Though the spire varies somewhat in its arrangement, no specimens have been found showing a trochoid spiral sufficiently elongate to be interpreted as intermediate to *P. neocomiensis*. With the possible exception of the nucleoconch, *P. trochoidea* is identical with *P. neocomiensis* in all characters which do not depend on the shape of the spire and its measurements. The nucleoconch is roughly oval, measuring about 0.15 × 0.1 mm. A median constriction probably indicates a former partition between the proloculus and deuterococonch. The

EXPLANATION OF PLATE 73

- Figs. 1-7. *Pfenderina neocomiensis* (Pfender) 1938; P. 43719-25; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, ×20. These separated specimens are mostly decorticated to a varying extent. Figs. 2, 3, and 6 show the serried septa with a large foramen in each, causing the appearance of a 'tunnel'. Fig. 3 is the most entire specimen and shows the apertural face. The slightly rugose appearance of this, not clearly seen in the photograph, is an indication of the numerous fine pores forming the cribrate aperture of the columella region. There is no aperture corresponding to the large foramen of each septum.
- Figs. 8-15. *Pfenderina trochoidea* sp. nov.; P. 43726-32, 42967; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, ×20. These picked specimens were found with those illustrated in figs. 1-7. The same general features can be seen, the best view of the apertural face being given by fig. 13.
- Fig. 16. *Kurnubia palastiniensis* Henson 1948; P. 42968; topotype specimen, ×20.
- Figs. 17-18. *Kurnubia wellingsi* (Henson) 1948; P. 42969-70; topotype specimens, ×20.
- Fig. 19. *Kurnubia jurassica* (Henson) 1948; P. 44637; topotype specimen, ×20.
- Fig. 20. *Arenobulimina?* sp.; P. 44638; Lower Cretaceous Thamama Group, Qatar Peninsula of Arabia, ×20. This specimen is illustrative of specimens that could be confused with *Pfenderina* or *Kurnubia*. Note the single, toothed, aperture and the absence of any area that could form a columella.
- Fig. 21. *Pfenderina trochoidea* sp. nov.; P. 43716; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, ×55.



chambers of the more trochoid specimens are similar to those of *P. neocomiensis*, being low, more or less oval, and possessing a narrow outer empty space and an internal part infilled with labyrinthine endoskeleton. The cribrate apertures and secondarily formed intercameral foramina are the same as those of *P. neocomiensis* but the infilling of the labyrinthic passages progressed more slowly, so that in section they are seen in about eight of the later chambers or even more. The shape of the apertural face is modified to a distorted horseshoe shape in the more planispiral specimens and the chambers tend to lose their overlap of the ventral pole of the axis of coiling. The infilling of the chambers therefore takes the form of a spiral, not that of a columella.

Remarks. *P. trochoidea* is so similar to *P. neocomiensis* in all characters not affected by the helicoid component of the coiling, that it is surprising that no intermediate specimens have been found. It is unlikely that the two species represent alternate generations of one population, because *P. neocomiensis* is found alone in rocks of later age. The ecological requirements of the two species seem to have been identical, and closely similar to those of *Kurnubia* spp.

Sixty-one separate specimens were found to be dextrally coiled and seventy sinistrally coiled. The ratio is not considered to differ significantly from 1:1.

Distribution. This species has been recorded only from the Middle East, in the Bathonian Uwainat member of the Araej formation, and in the Oxfordian–Callovian Najmah formation. In both cases it occurs with *P. neocomiensis* but wholly below all occurrences of *Kurnubia* spp. Records of *Pfenderina* sp. in the Bathonian Muhaiwir formation of Iraq and in groups *e* and *f* of the Lower Musandam Limestone of Jebel Hagab, Oman, which are also dated as Bathonian, may include this species.

GENUS KURNUBIA Henson 1948 (1947) emended

Plate 73, figs. 16–19; Plate 76, figs. 1–8

Type species. *Kurnubia palastiniensis* Henson 1948 (1947).

Emended diagnosis. The test is trochoid to strongly helicoid in known species, sometimes with a uniserial termination developing ventrally along the axis of coiling. The chambers are low and oval in shape in the spiral stage, each occupying most of the base. Each has a cellular subepidermal layer opening into a narrow empty space, inside which is a central labyrinthine zone. The overlap of the chambers over the ventral axis causes the labyrinthine parts of the chambers to aggregate to form a columella. In the uniserial stage the chambers are circular, but otherwise similar to those of the spiral stage. The aperture is cribrate, with small pores, and overlies and connects with that part of the chamber which is infilled with labyrinthine endoskeleton. This area tends to be proportionally larger in uniserial chambers than in spiral ones. There is usually little or no secondary infilling of the labyrinthine passages of the earlier chambers. Sections show what appear to be secondary intercameral foramina against the columella but the complexity of the structure makes them difficult to distinguish with certainty and their presence needs to be confirmed by observation on good solid specimens.

Remarks. The shell material was probably originally microgranular and imperforate